

Low latitude habitat use patterns of a recovering population of humpback whales

MARIA ISABEL CARVALHO GONÇALVES^{1,2}, RENATA SANTORO DE SOUSA-LIMA²,
NIEL NASCIMENTO TEIXEIRA³, MARIA EMILIA MORETE^{4,5}, GUSTAVO HENRIQUE DE CARVALHO^{1,6},
HARILDON MACHADO FERREIRA^{1,7} AND JULIO ERNESTO BAUMGARTEN^{7,8}

¹Graduate Program in Ecology and Biodiversity Conservation, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil, ²Laboratory of Bioacoustics, Department of Physiology and Behaviour, Biosciences Centre, Universidade Federal do Rio Grande do Norte, C.P.1511, CEP 59078-970, Natal, Rio Grande do Norte, Brazil, ³Department of Agricultural and Environmental Sciences, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil, ⁴Instituto Baleia Jubarte, Rua Barão do Rio Branco, 125, CEP 45900-000, Caravelas, Bahia, Brazil, ⁵VIVA Baleias, Golfinhos e cia, Rua Passo da Pátria, 1151, apto 81 B, CEP 05085-000, São Paulo, São Paulo, Brazil, ⁶Department of Botany, Universidade Estadual Paulista, Av. 24-A 1515, CEP 13506-900, Rio Claro, São Paulo, Brazil, ⁷Applied Ecology and Conservation Lab, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil, ⁸Department of Biological Sciences, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil

The coast of Brazil is an important low latitude nursery ground for humpback whales (Megaptera novaeangliae). The number of humpback whales in this region has increased and its population is reoccupying areas where it has been depleted during the whaling period. The goal of this study was to conduct land-based observations during 2014 and 2015 to characterize patterns of habitat use and relative abundance of humpback whales that migrate to one of these reoccupation areas: Serra Grande, Bahia state. The observed mean group size was 2.12 ± 0.96 individuals and did not vary through the reproductive season nor between years. Dyads (32.9%) and singletons (26.7%) were more frequently observed, and groups with calves represented 21.2% of the sightings. The mean number of whales counted per hour increased from 2014 (3.44 ± 3.35) to 2015 (5.12 ± 4.18). Habitat use varied during the season; whales used shallower waters closer to shore as the season progressed. The spatial distribution of groups with calves was dependent on the presence and number of escorts. Spatial segregation of groups with calves closer to shore is a key factor in understanding the overall distribution of whales in the area, suggesting that social strategies are affected by environmental factors, as seen in other wintering grounds. Small-scale studies from land-based stations, in areas such as this where there is no previous knowledge about the species, are cost effective. They provide information about the overall behavioural and spatial patterns while anthropogenic activity is still low, allowing habitat protection and management decisions before implementation and increase of human activities.

Keywords: Humpback whale, land-based observation station, habitat use, distribution, depth, occurrence

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INTRODUCTION

Humpback whales (*Megaptera novaeangliae*, Borowski 1781) have characteristic temporal and spatial migratory patterns that enable the species to take advantage of the great productivity of high latitude waters for feeding during the austral summer, and breeding and calving in low latitudes during the winter months. Winter coastal distribution (Dawbin, 1956; Clapham, 2000) associated with islands and reef systems (Clapham, 2009) is common in many humpback whale populations. Females with calves occur even closer to shore in shallower and more protected waters (Whitehead & Moore, 1982; Smultea, 1994; Ersts & Rosenbaum, 2003). Low latitude warmer waters (Clapham, 2000) with low predation risk (Corkeron & Connor, 1999) are thought to enhance the chances of survival of humpback whale newborn calves.

The population that migrates to the Brazilian coast between July and November (Martins *et al.*, 2001) is part of Breeding Stock A (IWC, 2005). This population feeds off South Georgia and Sandwich Islands (Zerbini *et al.*, 2006, 2011; Engel & Martin, 2009) which are ~4000 km distance from this breeding ground (Stevick *et al.*, 2006).

The number of humpbacks that migrate to Brazil is increasing (Freitas *et al.*, 2004; Andriolo *et al.*, 2010; Bortolotto *et al.*, 2016). For years, all research efforts were focused in the Abrolhos region (Martins *et al.*, 2001; Morete *et al.*, 2003), which continues to be the main breeding area (Andriolo *et al.*, 2006; 2010). However, the species occurs along the entire north-eastern coast of Brazil (Zerbini *et al.*, 2004; Lunardi *et al.*, 2008) and the population shows a significant expansion northern of Abrolhos, reoccupying winter areas (Rossi-Santos *et al.*, 2008; Andriolo *et al.*, 2010) used before the whaling period (Morais *et al.*, 2016). Surveys carried out between 2002 and 2005 showed a gradual increase in the Brazilian population reaching 6404 individuals in 2005 (Andriolo *et al.*, 2010). Bortolotto *et al.* (2016) had estimated

Corresponding author:
M.I.C. Gonçalves
Email: misabelgoncalves@gmail.com

19,429 humpback whales in 2012, while Pavanato *et al.* (2017) had estimated 12,123 individuals in 2015 using different methodologies in a larger study area. The IUCN (International Union for the Conservation of Nature) has changed the species status from 'vulnerable' to 'least concern' (IUCN, 2013) due to the increase in size of most humpback whale populations worldwide.

Zerbini *et al.* (2004) surveyed the north-east of Brazil and found most humpback whale sightings to occur within 50 m depth, which normally is associated with proximity to the coastline. In Brazil, previous studies mainly occurred in two regions along the state of Bahia: (1) the Abrolhos Bank located off the southern limit of the state and considered to be a unique environment compared with other regions along the coast and (2) Praia do Forte to the north. There is a gap of knowledge about the species between these two regions, where our study site is located, between Itacaré and Ilhéus, and where few human activities currently occur. The region is unexplored except for a few boat-based and aerial scientific surveys (Rossi-Santos *et al.*, 2008; Andriolo *et al.*, 2010; Baracho-Neto *et al.*, 2012). Between 2002 and 2005, during aerial surveys aimed at estimating the humpback whale population along the Brazilian coast, the Itacaré/Ilhéus region presented densities between 0.010 and 0.026 individuals per km² while over the Abrolhos Bank densities were between 0.028 and 0.091 individuals per km² (Andriolo *et al.*, 2010).

The presence of whales close to shore and the shoreline features that include an elevated point (Serra Grande), allowed observations from a land-based station (Würsig *et al.*, 1991). This research methodology has been applied to study humpback whales for two decades in the Abrolhos archipelago (Morete *et al.*, 2003, 2008), which is located within the Abrolhos Marine National Park. Our aim in this study was to characterize patterns of relative abundance and habitat use throughout the winter season in Itacaré/Ilhéus region from a land-based station located at Serra Grande. Social strategies used during the reproductive season and other unknown aspects of humpback whale distribution in this region will provide information to support better habitat protection and other management decisions.

MATERIALS AND METHODS

Study site

Data were collected from the highest point of Serra Grande (14°28'30"S 39°01'50"W), ~34 km north from the city of Ilhéus, southern Bahia state, north-eastern Brazil (Figure 1). The land-based station is located 315 m from the coastline at an elevation of 93 m above mean sea level. We considered a radius of 14 km from the observation point to define the

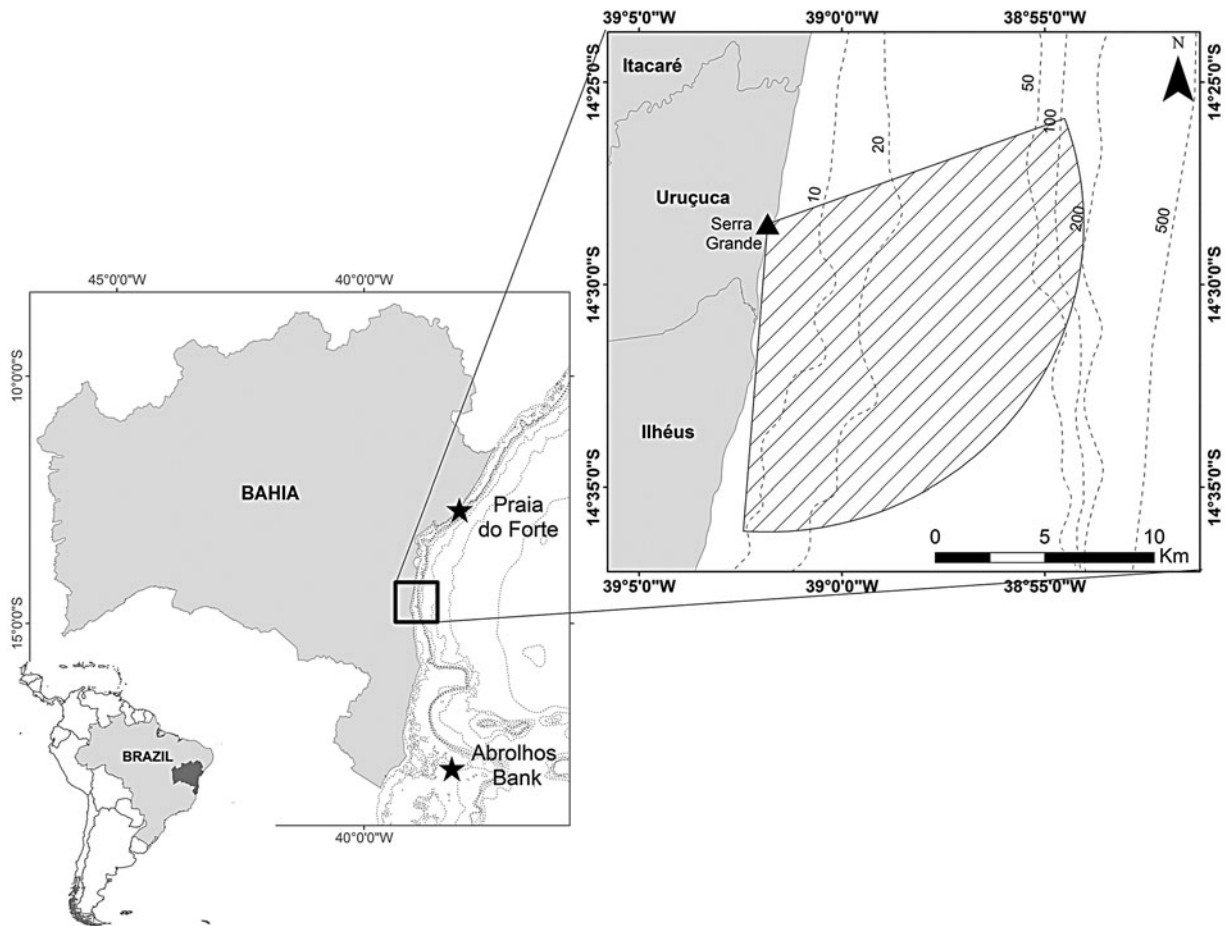


Fig. 1. Serra Grande study site located in north-eastern Brazil where a land-based observation station at elevation 93 m was used to conduct visual surveys that covered an area of 195.63 km² (striped area).

study area between 70 and 184° (True) covering 195.63 km². The orientation of the coastline, and the existence of vegetation and rocks prevent the monitoring of the north-east of the area.

The region's ocean floor is predominantly made of rocks and sand (Freire & Dominguez, 2006). Mean water temperature varies during the year between 24 and 29°C (NOAA, 2016).

Visual surveys

Observations were made between July and October in 2014 and 2015. Data collection was conducted during the daytime between 07:20 and 16:05 h following survey methods described by Mann (1999), each survey being of 1 h duration (Morete *et al.*, 2007, 2008). Morning and afternoon surveys were undertaken when weather conditions allowed good visibility of the skyline and when sea state was equal or below Beaufort 4. The mean interval between surveys was 3.22 h (SD = 0.68) allowing for observed groups to have moved away by the time of the second survey, leading to sample independence (Frankel & Clark, 2002).

Each survey was conducted by two or three dedicated observers and active search done with naked eye and binoculars 7 × 50. Whales were located based on presence cues such as blows, water splash from aerial behaviours, or exposure of a body part (Morete *et al.*, 2008). When a group of whales was sighted, the main observer (same person throughout the study) tracked and monitored the group using a total station TOPCON ES105 with 5' of precision and 30-power monocular magnification until the location angle, size, composition and behaviour of the group was identified (Morete *et al.*, 2008). Meanwhile, the other observers kept monitoring the area, searching for other whale groups.

In order to avoid counting groups twice, if there was any doubt about the discrimination of sighted groups during a survey, the effort was interrupted and the ongoing survey would be cancelled and another one started (Morete *et al.*, 2008). At the start and end of each survey and any time that conditions changed, the wind direction, cloud cover and Beaufort Sea state were registered by the main observer.

Definitions

A group was defined as a single or several individuals moving in coordination towards the same general direction no more than 100 m apart from each other (Whitehead, 1983; Morete *et al.*, 2008).

Group composition categories were defined as (a) mother with calf (MOC), (b) mother and its calf accompanied by an escort (MOCE), (c) mother and its calf accompanied by two or more escorts (MOCE/+), and in the absence of a calf, group definitions were based on the number of individual whales, (d) solitary (1AD), when a lone adult was observed, (e) two adults (dyad) or (f) more than two adults (multiple) (Morete *et al.*, 2007; Dunlop *et al.*, 2008). When it was not possible to determine the composition, the group was identified as 'undetermined'. The distance to the sightings did not allow the discrimination of juveniles, therefore we considered only two age classes: adults and calves, the latter identified as such when its length was up to 50% that of an adult (Chittleborough, 1953).

Spatial analyses

The total station TOPCON ES105 allows measurement of horizontal angles between two points, a known reference point and the target object, and also the vertical angle between the target object and the observer (Gailey & Ortega-Ortiz, 2002; Bailey & Lusseau, 2004). Total station and reference point Universal Transverse Mercator (UTM) coordinates were determined by GNSS (Global Navigation Satellite System) positioning, with a precision of 1.00 mm. Orthometric altitudes of these points were determined using Geoidal MAPGEO 2010 model (Monico, 2008). These point locations added to the height of the installed total station and tidal variation allowed calculations of UTM (E, N) coordinates of all points measured using trigonometric equations (Gonçalves, 2017). Errors due to Earth curvature (Vanicek & Krakowski, 1996) were corrected by transforming the horizontal distances to spherical distances.

Depth at the locations where groups were sighted were obtained by ArcGIS 9.3 Extraction tool of the Spatial Analyst using bathymetric information constructed from vectorization of nautical charts 1200 and 2105 from the Brazilian Navy (CHM, 2011–2015) followed by interpolation of depth values using ordinary kriging geostatistical analyses (Childs, 2004). Distance to coastline was calculated through the distances between the meridians of the position of the sighted group and the coast using Google Earth in order to acquire more precise values given the high resolution mapping and detailed images of the coast.

Statistical analyses

GROUPS

In order to examine how group size varied in the area throughout the season, we considered only the data from groups for which size and composition were determined with confidence. A generalized linear model (GLM) was used to fit the group size data into a Poisson distribution. Year and Julian day were used as predictors of group size.

RELATIVE ABUNDANCE

Because of the fluctuation of whale relative abundance between seasons (Morete *et al.*, 2008), the peak of each season was calculated using a segmented regression (Muggeo, 2008) of the whale counts per survey. The seasons were divided into three periods (initial, middle and final) within a calving season of 123 days, each period having 41 days (Morete *et al.*, 2007), and the peak of the season being the centre of the middle period, which varied depending on the year. Due to the lack of normality of the distribution, we used a Mann–Whitney U test to verify if hourly whale counts changed between the sampled years (2014 and 2015). A GLM was used to fit the number of whales sighted per hour (number of adults and calves separately) into a Poisson distribution and test if it changed as the season progressed. The model to explain adult relative abundance included year and lunar phase (four categories considered by NOAA) as categorical predictors and Julian days and sea state (Beaufort 1 to 4) as continuous predictor variables, as well as the interaction between the variables: year and Julian days. The model to explain calf abundance also included number of adults as a predictor variable. The number of individuals considered in undetermined groups was the maximum

number of sighted animals to avoid underestimation of the total number of whales in such cases. The residuals and the residual variation were verified to ensure that the models were adequate with respect to the premises.

HABITAT USE

An ANOVA followed by a Tukey's honest significant difference (HSD) test was used to verify if a whale group's mean distance to coast and depth were different among periods of the season. Spatial distribution of groups in the sampled area along the season was mapped as Kernel densities using Hawth's Tools developed as an extension of ArcGIS (Beyer, 2004). We used default values for the parameters within this tool and the band (h) was defined as 1.0 km to smooth over 100×100 m surface cell size using the normal bivariate method. For comparison of the maps among the different periods, the values were normalized to a common scale (0–1). Statistical transformation was applied on a logarithmic function that rescaled the values maintaining the original form of distribution. We used t tests to establish whether distance to coast and depth were different between groups with and without calves. Within groups with calves, such differences were tested between MOC, MOCE and MOCE/+ using ANOVA. Mother and calf groups (MOC) were defined as the baseline to verify differences with MOCE and MOCE/+. We did not find any significant deviations from normality given the robustness of the analyses to deviations from this assumption. Variances were also assumed to be equal in all ANOVAs except those used to test depth differences between groups with calves. In those cases, we used ANOVAs with Welch's correction for unequal variances. All statistical analyses were run in R 3.0.2 (R, Development Core Team) with the significance value (α) of 0.05.

RESULTS

Ninety-three hours of surveys (Table 1) were carried out during 67 days in the field (37 days in 2014, and 30 in 2015). The identification of the number of individuals and age class (adult or calf) in the groups was possible for 146 (67.59%) out of the 216 groups sighted. Adult individuals were the majority ($N = 278$) compared with calves ($N = 31$).

Groups

Group size varied from a single individual to five whales. Mean group size was 2.12 ($SD = 0.96$). Year and day of the season did not affect group sizes (Table 2).

The most common group composition was dyad 32.9% ($N = 48$), followed by solitary individuals 26.7% ($N = 39$) and groups with calves 21.2% ($N = 31$). Multiple groups were the least common in the area (19.2%, $N = 28$). Groups

Table 1. Number of surveys performed with the number of field days in parentheses by period of the season from a land-based observation station in 2014 and 2015 in Serra Grande, Bahia state, Brazil.

	Initial	Middle	Final	Total
2014	18 (11)	14 (10)	20 (16)	52 (37)
2015	9 (7)	19 (13)	13 (10)	41 (30)

Table 2. Generalized Linear Model (Poisson distribution) parameter estimates and P -values for year and Julian day that explained group sizes of humpback whales observed from a land-based observation station in 2014 and 2015 in Serra Grande, Bahia state, Brazil.

	Estimate	P -value
Intercept	142.828946	0.538
Year	-0.070815	0.539
Julian day	0.002376	0.327

with a calf were comprised mostly of MOC (61.3%, $n = 19$), MOCE (22.6%, $N = 7$), and MOCE/+ (16.1%, $N = 5$) categories.

Relative abundance

Abundance in both 2014 and 2015 seasons was characterized by a segmented distribution with the break point between the end of August and beginning of September (Figure 2). The peak for 2014 was 23 August and for 2015, 4 September. The segmented regression model was significant ($P < 0.001$) and the regression coefficient was positive for the first half and negative for the second half. Adult hourly abundance pooled for both years varied from 0 to 14 and calves from 0 to 4 individuals. The maximum hourly abundance (17 individuals) was observed in the beginning of September 2015.

In 2015, the mean number of individuals per hour ($N = 5.12$, $SD = 4.18$) was significantly greater ($W = 809$, $P < 0.05$) than in 2014 ($N = 3.44$, $SD = 3.35$). This difference was due to the higher number of adults observed per hour ($W = 813$, $P < 0.05$) in 2015 ($N = 4.68$, $SD = 3.74$) when compared with adult numbers in 2014 ($N = 3.19$, $SD = 3.13$). The number of calves did not change significantly between years ($W = 949$, $P = 0.24$) although the absolute counts were higher in 2015 ($N = 0.44$, $SD = 0.8$; $N = 0.25$, $SD = 0.52$ in 2014).

Based on GLM, adult number was affected by the year ($P < 0.05$) and lunar phase. The full moon was considered as the baseline lunar phase in the model and there were significantly fewer adults in the area during the new moon ($P < 0.001$) and first quarter ($P < 0.01$) but no significant difference was verified during the last quarter ($P = 0.33$). The interaction between Julian day and year also influenced the adult numbers ($P < 0.05$); different peaks in adult abundance occurred between the years and a sharper decrease in the adult numbers beginning in the end of September was observed for 2015 when compared with 2014. Sea state did not affect adult humpback whale abundance (Table 3).

Number of calves was positively affected by the Julian day ($P < 0.01$) and by the number of adults ($P < 0.001$). Year, lunar phase and sea state did not affect the number of calves (Table 4).

Habitat use

Depth increases as a function of distance from the coast and beyond 11 km this effect is higher (Figure 3). The majority of humpback whale groups (90.3%) were sighted in waters of less than 50 m depth and 67.6% up to 10 km away from the coast. Mean distance to coast gradually decreased through the season ($F = 22.22$, $d.f. = 139$, $P < 0.001$; Table 5, Figure 4) and was significantly different between

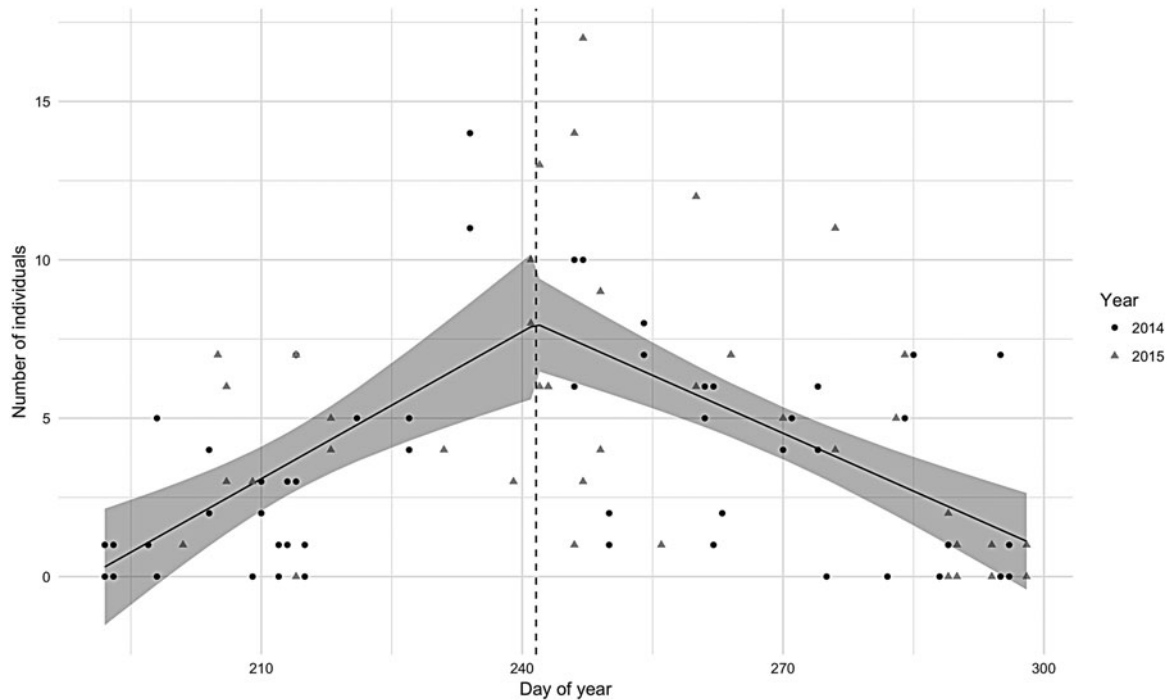


Fig. 2. Hourly number of humpback whales observed in Serra Grande (Bahia state, Brazil) along the Julian days in 2014 (dots) and 2015 (triangles) with the segmented regression 95% confidence interval model showed in grey.

initial and middle periods ($P < 0.01$) and between initial and final periods ($P < 0.001$), but not significant between middle and final periods ($P = 0.07$). Similarly, mean depth values in which whales occurred varied among periods ($F = 23.08$, $d.f. = 139$, $P < 0.001$; Table 5), decreasing as the season progressed, being significantly different between the initial and middle periods ($P < 0.001$) and between initial and final periods ($P < 0.001$). No significant differences in mean depth of humpback whale sightings were observed between middle and final periods of the season ($P = 0.23$).

Mean values for distance to coast were significantly greater ($t = 5.2019$, $d.f. = 39.588$, $P < 0.001$) for groups without calves (8.78 ± 2.33 km) than for groups with calves (5.58 ± 3.19 km). Within groups with calves, the distances where

each group type were sighted were significantly different ($F = 7.161$, $d.f. = 29$, $P < 0.05$). Groups of MOC were sighted significantly closer to the coast than MOCE/+ ($P < 0.05$) but no significant differences between MOC and MOCE ($P = 0.08$) were found (Table 6).

We found significant differences in mean depth for groups with and without calves ($t = 4.3084$, $d.f. = 47.079$, $P < 0.001$). Groups with calves were in shallower waters (22.38 ± 12.67 m) than groups without calves (33.41 ± 12.28 m). Also, there were significant differences in the mean depth of sightings of the different types of groups with calves ($F = 6.2516$, $num. d.f. = 1.000$, $denom. d.f. = 14.625$, $P < 0.05$): MOC were sighted in shallower waters than MOCE ($P < 0.05$) and MOCE/+ ($P < 0.05$) (Table 6).

Table 3. Parameter and P -values estimated using a Generalized Linear Model with Poisson distribution that explained adult relative abundance observed from a land-based observation station in 2014 and 2015 in Serra Grande (Bahia state, Brazil). Predictor variables were: year, Julian day, sea state (Beaufort), lunar phase and the interaction between Julian day and year.

	Estimate	P -value
Intercept	0.762771	0.21979
Year 2015 ^a	2.245929	0.01161*
Julian day	0.001787	0.45461
Sea state	0.108550	0.09855
First quarter ^b	-4.430749	0.00268**
Last quarter ^b	-0.141395	0.33329
New moon ^b	-0.700321	0.00002***
Year 2015 ^a × Julian day	-0.007732	0.03253*

P -values: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

^aDifference from 2014.

^bDifference from full moon.

Table 4. Parameter and P -values estimated using a Generalized Linear Model with Poisson distribution that explained calf relative abundance observed from a land-based observation station in 2014 and 2015 in Serra Grande. Predictor variables were: year, Julian day, sea state (Beaufort), lunar phase, number of adults and the interaction between Julian day and year.

	Estimate	P -value
Intercept	-11.21738	0.00368**
Year 2015 ^a	3.93766	0.37122
Julian day	0.03663	0.00644**
Sea state	-0.43180	0.07253
First quarter ^b	0.52168	0.35213
Last quarter ^b	0.16947	0.76678
New moon ^b	-0.15624	0.83201
Adults	0.24152	0.00001***
Year 2015 ^a × Julian day	-0.01379	0.40563

P -values: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

^aDifference from 2014.

^bDifference from full moon.

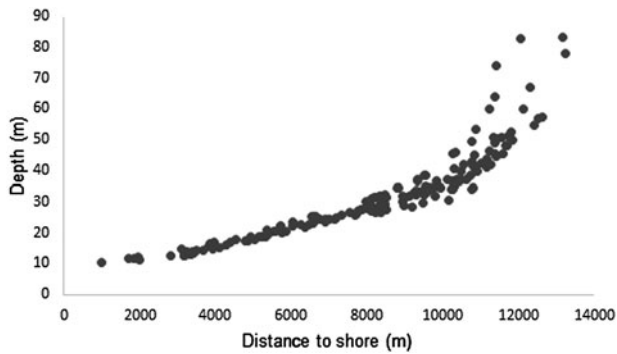


Fig. 3. Relationship between distance to coast and depth of humpback whale groups sighted from a land-based observation station in 2014 and 2015 in Serra Grande, Bahia state, Brazil.

Table 5. Descriptive statistics (mean \pm SD) for distance to coast and depth values of humpback whale groups sighted from a land-based observation station in Serra Grande (Bahia state, Brazil) per periods of the season (initial, middle, final) in the years 2014 and 2015.

	Initial	Middle	Final
Distance to coast (km)	10.10 \pm 2.12	7.98 \pm 2.70	6.76 \pm 2.97
Depth (m)	41.55 \pm 13.93	29.79 \pm 11.58	25.74 \pm 11.87

DISCUSSION

To our knowledge, this is the first study describing the habitat use patterns of humpback whales in Serra Grande coastal low latitudes. Descriptions of baseline habitat use patterns in coastal areas while there is a low level of human disturbance are essential for humpback whale conservation, in particular where overlap with human activities may occur in the future, such as the construction of a new port in the region (BAMIN, 2011).

Group characteristics

Mean humpback whale group size in Serra Grande was similar to that observed in other calving areas such as Abrolhos in Brazil (Martins *et al.*, 2001), Ecuador (Scheidat *et al.*, 2000; Félix & Haase, 2001) and the east coast of Australia (Franklin *et al.*, 2011). We did not observe variation in group sizes through the season nor between the two

sampled years as also occurred in Abrolhos (Morete *et al.*, 2007). Nonetheless, in Hawai'i (Baker & Herman, 1984) and in Ecuador (Félix & Haase, 2001), group sizes tend to increase as the season progresses due to an increase in mature male densities searching for receptive females in competitive groups. Each population might have different social strategies depending on site-specific contexts or even on culture.

The proportions relating to group composition observed are identical to the areas surveyed north of Serra Grande (Lunardi *et al.*, 2008; Rossi-Santos *et al.*, 2008). The proportion of groups with calves is much smaller in Serra Grande (21%) than around the Abrolhos Archipelago (48%) (Morete *et al.*, 2007), which is within the main calving ground for the population that migrates to Brazil. Also, the proportion of mother-calf pairs escorted by a single adult (MOCE) is much higher in Abrolhos (Morete *et al.*, 2007), and may be related to the geomorphological characteristics as further discussed.

Relative abundance patterns

It is not surprising that the number of whales sighted has increased from 2014 to 2015 since the Population Stock A has risen in recent years (Andriolo *et al.*, 2010; Bortolotto *et al.*, 2016).

The peak of the season varied between years; in 2015, it was 12 days later than in 2014. Nevertheless, there was a marked decrease in the number of whales observed in late September in 2015. These temporal fluctuations in relative abundance have been observed in other humpback whale reproductive areas (Baker & Herman, 1981; Corkeron *et al.*, 1994; Mattila *et al.*, 1994; Frankel & Clark, 2002; Morete *et al.*, 2008) and may be related to migratory triggers in low and high latitudes. Dawbin (1966) suggests that photoperiod plays a role in migratory timing in high latitudes. Sea surface temperature (Nishiwaki, 1959) and food resource availability in the previous summer (Craig *et al.*, 2003) are thought to be the most important factors that trigger humpback whale migration to the feeding grounds (Abrás, 2014). The fat layer accumulated from summer feeding prior to migration to low latitudes would limit the permanence of individuals in their reproductive areas (Craig *et al.*, 2003). In Brazilian waters, the 'El Niño' phenomenon caused an increase in the sea surface temperature in 2015 (NOAA, 2016). The temperature rise started in August 2015 and could have affected the timing of return of humpback whales to

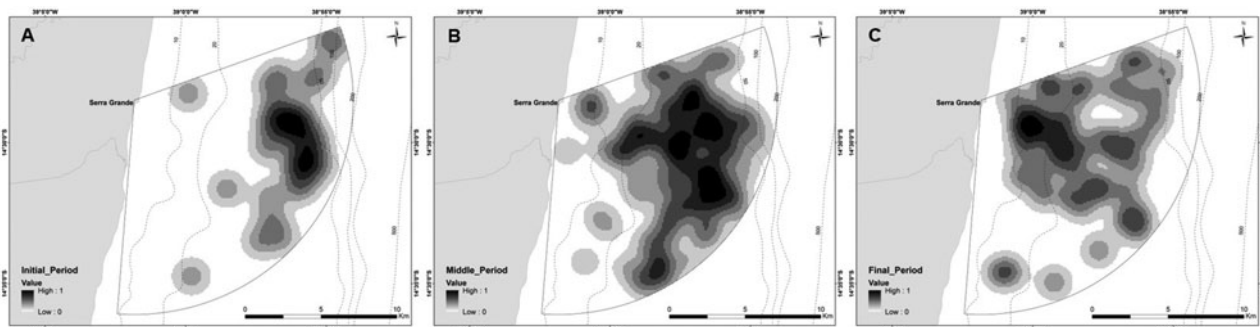


Fig. 4. Kernel density maps of all groups of humpback whales sighted in 2014 and 2015 from a land-based observation station at Serra Grande (Bahia state, Brazil) divided by periods of the season: (A) initial; (B) middle; (C) final.

Table 6. Mean and SD of distance from coast and depth of the humpback whale groups with calves observed in 2014 and 2015 in Serra Grande, Brazil (MOC = mother and calf, MOCE = mother and calf and one escort, MOCE/+ = mother and calf and two or more escorts).

	Distance to coast (km)	Depth (m)
MOC	4.47 ± 2.71	17.72 ± 7.85
MOCE	6.76 ± 3.41	28.80 ± 18.44
MOCE/+	8.15 ± 3.04	31.12 ± 12.06

Antarctica, explaining the sharp decrease in abundance after the peak of the 2015 season.

Highest adult abundance coincided with full and last quarter lunar phases. Lunar phase affects when males are more likely to sing during the day in Abrolhos (Sousa-Lima & Clark, 2008). In Angola, lunar phase affects the relative abundance of singers (Cerchio *et al.*, 2014), the authors detecting fewer singers during full moon than at new moon. Humpback whale singers are often characterized by slow-moving individuals (Tyack & Whitehead, 1983; Spitz *et al.*, 2002; Noad & Cato, 2007) and thus less likely to be detected by visual surveys (Noad & Cato, 2007) when compared with passive acoustic monitoring (Frankel *et al.*, 1995; Noad & Cato, 2007). One of the possible reasons for differences in number of whales counted by us during the new moon could be that the behaviour of singing males makes them harder to be detected from a land-based observation station, and we might have underestimated the number of adults by missing singers during the new moon. Alternatively, maybe the song keeps other acoustic competitors further away, consequently leading to the presence of a smaller number of individuals, or the low densities lead to males singing more to attract females. Studies on the abundance of singers in the area may elucidate these findings.

The number of calves increased throughout the season, the same pattern observed in Abrolhos, where the number of calves varied with the number of adults and the Julian day (Morete *et al.*, 2003). Surprisingly, the number of calves did not increase from 2014 to 2015, differing from what was observed for adults. Morete *et al.* (2008) surveyed the Abrolhos Archipelago for 7 years, and noted an increase in the number of adults but the number of calves remained the same, and only increased significantly in the last year sampled. During the same years, Morete *et al.* (2007) did not find evidence that the number of adults in the groups observed in Abrolhos increased over the years, concluding that females with calves could be using different areas or that the number of calves would be the result of falling birth rates. Clapham (1996) suggests that reproductive rates may be affected by food availability, as was also proposed by Seyboth *et al.* (2016) for reproductive success of the southern right whales. Therefore, the constant number of calves observed between 2014 and 2015 could be a result of lower food availability in the 2014/2015 summer feeding ground or a change in preferred calving area by females in 2015.

Bad weather conditions that result in high sea state levels (Beaufort scale) may reduce whale detection probability (Corkeron *et al.*, 1994). Nonetheless, when observations were restricted to sea state up to Beaufort level 4, the number of adults and the number of calves sighted in Serra Grande were not affected. Smultea (1994) had a limit for data collection of up to Beaufort 3 and also did not find any

effect of sea state on detection rates. Frankel & Clark (2002) found that the sighting rate was negatively affected by the sea state when working up to Beaufort 6, and noted this effect particularly applied in offshore areas. There is a trade-off between the amount of data collected (considering higher sea state levels) and quality and reliability of sightings (missed detections).

Social organization and habitat use

Distribution of whales varied throughout the season, with groups using waters closer to the coast as the season progresses, as also observed in Western Australia by Jenner *et al.* (2001), who suggested that the migratory route from the feeding areas to the calving ground would be further away from the coast and the path back to the feeding ground would be closer to the coast. The same pattern may be occurring off Serra Grande. Also, another reason that could explain this approximation is the spatial segregation of groups with and without calves that was identified in Serra Grande. The increase in the number of calves after the peak of the season may have caused the groups to stay closer to the coast as the season progressed.

Coastal areas such as Serra Grande, where the shelf break is closer to shore and depth changes abruptly, lead to more concentration of mother and calf groups than areas where depth varies gradually, such as off islands and archipelagos. In Serra Grande, the difference in mean depth between the sightings of groups with and without calves is around 10 m, and in Abrolhos is smaller than 5 m (Martins *et al.*, 2001), where mean depth is 30 m, perhaps allowing escorts to have easier access to mothers and calves. Different habitat conditions across the range of humpback whales in Brazil may lead to differences in habitat use and social organization as observed in other populations (Félix & Botero-Acosta, 2011).

Groups with calves occupying shallower waters closer to shore are considered a social strategy (Ersts & Rosenbaum, 2003). Mothers could be protecting their calves against harassment from males trying to mate with them (Smultea, 1994), which may cause injury to the newly born calves (Baker & Herman, 1984) as well as higher energy costs for both mother and calves (Cartwright & Sullivan, 2009; Craig *et al.*, 2014). Parental care could also explain why mothers remain closer to shore in shallow waters where there are fewer predators (Smultea, 1994), less turbulence (Whitehead & Moore, 1982), and shallower depth, limiting the approach and manoeuvre of males (Ersts & Rosenbaum, 2003; Bruce *et al.*, 2014). However, females with calves may allow the presence of an escort during transit in areas where they would be exposed to deeper, less protected waters (Ersts & Rosenbaum, 2003). An escort may offer protection to the mother-calf pair (Herman & Antinaja, 1977), which was evidenced by the observations of escorts defending calves from predator attacks (Pitman *et al.*, 2015), acting as bodyguards (Mesnick, 1996; Wilson & Mesnick, 1997; Cartwright & Sullivan, 2009), or even protection from other males attempting to mate.

Groups with calves escorted by adults occur in deeper waters (Betancourt *et al.*, 2012; MacKay *et al.*, 2016) and in Serra Grande, as the number of escorts increases, the distances from shore increase. Craig *et al.* (2014) and Félix & Botero-Acosta (2011) observed similar results and suggested that water depth not only limits the association of escorts to

mother-calf pairs but would also limit the movement of courting males. Larger groups with calves would comprised inexperienced mothers that are unable to avoid being joined by multiple escorts (Elwen & Best, 2004). Distance to coast and water depth are environmental factors that explain the distribution of humpback whale groups. Thus, our results support the interaction between environmental constraints and social organization proposed for the species (Félix & Botero-Acosta, 2011).

CONCLUSION

Serra Grande has a lower percentage of groups with calves compared with Abrolhos, but this percentage is comparable to other reproductive grounds (Ersts & Rosenbaum, 2003; Rasmussen *et al.*, 2011). Habitat use patterns also support the notion that this is a calving area because of the typical increase in the abundance of calves as the season progresses. As populations recover, the presence of humpback whales in other low latitude areas tends to expand. The importance of Serra Grande as a calving area will probably increase given the uniqueness of this site in having the shortest distance to the shelf break in Brazil (IBGE, 2011; Prates *et al.*, 2012), allowing humpback whales to concentrate very close to the coast. It is noteworthy that despite being a small-scale study, we observed the same pattern as found in larger scale studies (Zerbini *et al.*, 2004), reinforcing this general pattern for humpback whales off Brazil. Land-based platforms in high altitude stations are cost effective and representative of habitat use patterns. These local efforts throughout the area of occurrence may reveal which environmental factors better explain humpback whale distribution and abundance on a larger scale. Decision making for the creation of protected areas (Andriolo *et al.*, 2010) and the implementation of human activities at sea will be supported by robust knowledge of site-specific abundance patterns, avoiding potential problems such as collisions with vessels (Redfern *et al.*, 2013) and site abandonment (Jones & Swartz, 2009). Additionally, the general public can profit from touristic activities by experiencing land- or boat-based whale watching.

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Correspondence should be addressed to:

M.I.C. Gonçalves

Graduate Program in Ecology and Biodiversity Conservation, Universidade Estadual de Santa Cruz, Rodovia Jorge Amado, km 16, CEP 45662-900, Ilhéus, Bahia, Brazil
email: misabelgoncalves@gmail.com